

EARLY LLANDOVERY TRILOBITES FROM WALES WITH NOTES ON BRITISH LLANDOVERY CALYMENIDS

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ABSTRACT. Some early Llandovery (Silurian) trilobites from Wales are described. The calymenids are compared with described British Llandovery species, including two samples from Girvan, Scotland. Principal components analysis is used to demonstrate both the variation in profile of the preglabellar area and the independent and dimorphic (thus probably sexual) variation in relative glabellar width of Llandovery calymenids. *Diacalymene crassa* Shirley and *D. marginata* Shirley differ considerably from *D. diademata* (Barrande) in the profile of the preglabellar area and form the end of a spectrum of variation among British Llandovery calymenids: they are provisionally referred to *Calymene* s.l. Characterization of the genus *Diacalymene* in terms of 'ridging' of the preglabellar area is considered to be vitiated (at least for internal moulds) by the intraspecific variability of this feature and the subjectivity of its recognition. Two species are tentatively distinguished among Welsh early Llandovery calymenids, *C. crassa* and another species similar to a sample from Newlands, Girvan. Seven other species of trilobites are briefly described.

THE present work forms part of a larger study of the early Llandovery shelly faunas of Wales. The term 'early Llandovery' is employed here in the sense of 'pre-Upper Llandovery' or 'pre-Fronian', since it is not yet possible on the basis of their shelly faunas alone to distinguish the Lower from the Middle Llandovery (Rhuddanian and Idwian). This paper describes trilobites unknown or poorly known in the fauna described from near Meifod, Montgomeryshire (Temple 1970). A complete listing of trilobites and brachiopods and an analysis of their distribution in the early Llandovery of Wales will be made when the brachiopod faunas have been fully described.

Trilobites form a numerically insubstantial part of Welsh early Llandovery shelly faunas. In fifty-six samples the number of trilobite cranidia and pygidia is only 2.6% of the number of brachiopod dorsal valves and ventral valves, and this low figure includes one locality unusually rich in trilobites (loc. 7132, with 19.5%). The most abundant trilobites are the calymenids, poorly represented at Meifod but more common in the Haverfordwest area of Pembrokeshire. Description of the Welsh early Llandovery calymenids, to which the major part of this report is devoted, has involved comparison with other British Llandovery members of the family.

LOCALITIES

Specimens described here are from the localities listed below. In the list each locality code number, by which the locality is referred to subsequently in the text (e.g. loc. 6701), is followed by the National Grid reference.

- 6701: SJ 1135 1013. 5.2 km SW. of Meifod, Montgomeryshire. This is the locality from which the fauna described earlier was collected (Temple 1970).
- 7001a: SJ 2358 1936. 3.5 km WNW. of Llandysilio, Montgomeryshire.
- 7004b: SJ 1957 1786. 6.2 km NE. of Meifod, Montgomeryshire.
- 7021b, c: SN 7622 3247. 1.8 km SSW. of Llandovery, Carmarthenshire.
- 7022a: SN 9531 5116. 1.5 km N. of Garth, Brecknockshire.

7029a: SN 9719 5324. 2.5 km S. of Llanafan-fawr, Brecknockshire.

7121: SM 9643 1473. 450 m SE. of Higgon's Well, Haverfordwest, Pembrokeshire.

7122, 7123, 7126, 7127, 7132, 7140, 7142c, 7148: SM 9573 1547 to SM 9582 1537. Lane leading to Gasworks, Haverfordwest, Pembrokeshire. 7122, 7123, 7140, and 7142c are in the lowest exposed 25 m of the Gasworks Mudstone; 7126, 7127, 7132, and 7148 are in the topmost 25 m of the Gasworks Mudstone.

PRESERVATION AND TECHNIQUES

Nearly all the material is preserved as internal and external moulds. For most trilobite families this preservation is excellent, but for the calymenids it gives rise to a particular problem. The rachial and preglabellar furrows are deep and often undercut, so that the deepest parts of the furrow fillings of external moulds break off and remain at the bottoms of the internal mould furrows. These furrow fillings can be removed by needle to produce excellent internal moulds, but the external moulds, which would normally provide evidence for the exterior surface of the cephalon, are always imperfect and lack the bases of the furrows. Detailed study of cranidia of Llandovery calymenids must therefore be based on internal moulds and, especially in the study of the preglabellar area, the methods used and the results obtained are not directly comparable with those based on exteriors.

Measurements have been made on a microscope with eye-piece graticule. Of the measurements made on calymenid cranidia, variates x_2 , x_3 , and x_4 , which relate to the profile of the preglabellar area, have been measured on silicone rubber casts made from internal moulds and sectioned in the sagittal plane. This method of measurement is essential for those specimens in which the base of the preglabellar furrow is obscured in profile view of the internal mould by the bulging of the preglabellar area backwards opposite the rachial furrows, but even when this is not the case it has been found difficult to measure the profile of the preglabellar area sufficiently accurately from internal moulds.

The original data of the calymenid cranidial measurements x_1 to x_5 have been deposited in the British Library, Boston Spa, Yorkshire, as supplementary Publication No. SUP 14004 (2 pages).

Principal components analysis, the technique used in analysing the calymenid cranidial measurements, is now so widely used for multivariate data in biology and palaeontology that a detailed explanation is not considered necessary here, the reader being referred to Seal's book (1964, p. 101) for an exposition of the technique. It should be noted that, even when not used as a basis for formal statistical tests, principal components analysis is a powerful pictorial technique for displaying the mutual relations of multivariate samples, and it is largely in this latter capacity that it is used here. In this respect, by depicting the simultaneous variation in several characters (before or after abstraction of a size factor represented by the first eigenvector), its superiority to bivariate plotting, which can deal only with characters taken in subjectively selected pairs, is indisputable. Furthermore, the mutual orthogonality of the eigenvectors in principal components analysis allows conclusions to be drawn about the independence of the variation represented by these eigenvectors (each of which involves several characters), as in the variation of relative glabellar width and of preglabellar profile. Principal components analysis of the correlation matrix is used in preference to that of the covariance matrix so as to remove the effects of the disparate sizes of the original variates, i.e. so that small variates (those relating to the preglabellar area) may contribute equally with large variates (glabellar length and width) to the total variance that is partitioned into the eigenvalues. As previously (e.g. Temple 1970, p. 6), the convention is continued of using x for the original variates and y for the variates transformed along the eigenvectors.

The plates which illustrate this paper were made up before agreement had been reached at the 1973 Oslo conference on a standard orientation of trilobites for

illustration (Temple, in press). The 'dorsal' view of calymenid cephalae and cranidia employed on the plates is obtained by setting horizontal the plane tangent to the crest of the pre-occipital glabella and the occipital ring. 'Normal projection', as used in the description of measurements, is projection at right angles to the line joining the ends of the measured structure.

Registration numbers of specimens prefixed by A are those of the Sedgwick Museum, Cambridge; those prefixed by HMA, of the Hunterian Museum, Glasgow; those prefixed by In or It, of the British Museum (Natural History), London; those prefixed by GSM, OTJ, TCC, or Zs, of the Institute of Geological Sciences, London.

Superfamily CALYMENACEA Milne Edwards, 1840

Family CALYMENIDAE Milne Edwards, 1840

Calymenid remains are most abundant at a high horizon in the Gasworks Mudstone at Haverfordwest (loc. 7132), although occasional specimens are known from other horizons in the Gasworks Mudstone, as well as from other areas.

The following calymenid species have been described from the Llandovery of Britain:

- (1) *Diacalymene crassa* Shirley, 1936 (p. 416, pl. 29, figs. 21–23). The only available topotypic specimen is the holotype (GSM 54910—figured here on Pl. 25, figs. 3–4), an internal mould of a cranidium, well preserved except that the occipital ring and fixed cheeks are broken and the preglabellar area is slightly abraded. The type locality is in the Gasworks Mudstone of the Haverfordwest area, but the precise horizon is unknown, and further collecting has not yielded more topotypic material. The paratype of *crassa* (GSM 54911) is not topotypic.
- (2) *Calymene replicata* Shirley, 1936 (p. 411, pl. 30, figs. 2–5). The holotype (A 14922a) consists of the internal mould of a cephalon, lacking the dorsal preglabellar area, with three thoracic segments attached; the counterpart external mould, of which a cast was figured by Shirley (pl. 30, fig. 2), is now missing from the Sedgwick Museum collections, so that the preglabellar area of the holotype cannot now be reconstructed. The type locality is near the base of the Upper Llandovery at Lletty'r-hyddod in the Llandovery area. Other topotypic specimens in the Sedgwick Museum (A 14923–14927) show the preglabellar area and also the thorax and pygidium (revealed by preparation of A 14923—Pl. 26, fig. 1) but not the hypostome. Some of the topotypes (although not the holotype) are distorted.
- (3) *Calymene planicurvata* Shirley, 1936 (p. 412, pl. 30, figs. 6–7). The holotype (GSM 19624) is an internal mould of a large cranidium, well preserved except for slight breakage of the preglabellar area and lack of the right fixed cheek. The type locality is Bog Mine, Shelve inlier, Shropshire (?Middle Llandovery). Additional topotypic specimens (cranidia and a pygidium) are available in the Institute of Geological Sciences and the British Museum (Natural History).

In addition to topotypic material of these species, the following calymenids have been used for comparative purposes:

- (1) Newlands Formation (Middle Llandovery), Newlands, Girvan, Ayrshire, Scotland (Gray Collection, British Museum (Natural History)). Material from this locality was referred by Shirley (1936, p. 411) to *C. replicata*. This collection

is extensive and well preserved, all parts of the exoskeleton being represented (Pl. 26, figs. 5-6, 9-10).

- (2) Mulloch Hill Formation (Lower Llandovery), Mulloch Hill, Girvan, Ayrshire (Gray Collection, British Museum (Natural History)). This material is not so extensive as that from Newlands but is well preserved (Pl. 26, figs. 2-4, 7-8).
- (3) Bank outlier, Round Hill, Shropshire (British Museum (Natural History)). Equivalent horizon to Bog Mine. A few small specimens.
- (4) Gasworks Mudstone, Haverfordwest, Pembrokeshire (Institute of Geological Sciences).

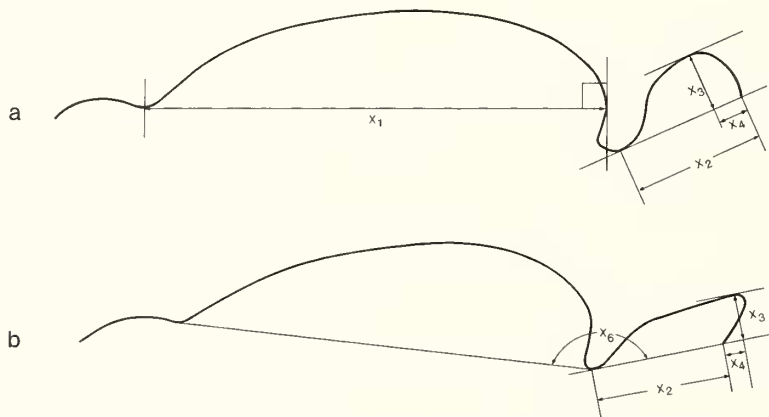
Measurements. The following measurements have been made (x_1 , x_5 to x_8 on internal moulds; x_2 to x_4 on sagittally sectioned silicone rubber casts of internal moulds):

Cranidia (text-fig. 1)

- x_1 = sagittal length of pre-occipital glabella (from deepest part of occipital furrow to plane tangential to steepest slope of anterior margin of glabella, normal projection);
- x_2 = sagittal length of preglabellar area (length of tangent in sagittal plane from rostral suture to surface of internal mould at or in front of preglabellar furrow, normal projection);
- x_3 = perpendicular distance between tangent of x_2 and parallel line in sagittal plane tangential to crest of preglabellar area;
- x_4 = sagittal distance (projected as x_2) between crest of preglabellar area (as defined by tangent in x_3) and rostral suture (positive if measured forwards as text-fig. 1a, negative if measured backwards as text-fig. 1b);
- x_5 = maximum transverse width of glabella across L_1 lobes (measured between parallel exsagittal vertical planes tangential to outsides of lobes, not at bases of rachial furrows);
- x_6 = angle subtended at base of preglabellar furrow by lines in sagittal plane to the base of the occipital furrow and to the rostral suture.

Pygidia

- x_7 = sagittal length (measured from deepest point of articulating furrow in front), normal projection;
- x_8 = transverse separation of bases of rachial furrows at abaxial ends of articulating furrow.



TEXT-FIG. 1a, b. Sagittal profiles (schematic) of internal moulds of calymenid cranidia showing measurements. Note (i) that x_4 is positive in the upper profile but negative in the lower one, (ii) that the points in the preglabellar furrow from which x_2 and x_6 are measured will not necessarily coincide, although they happen to do so in the lower profile.

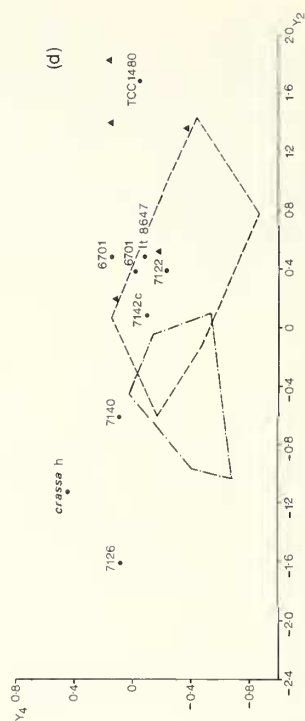
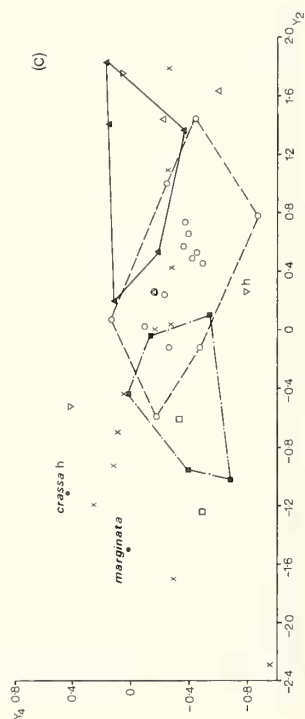
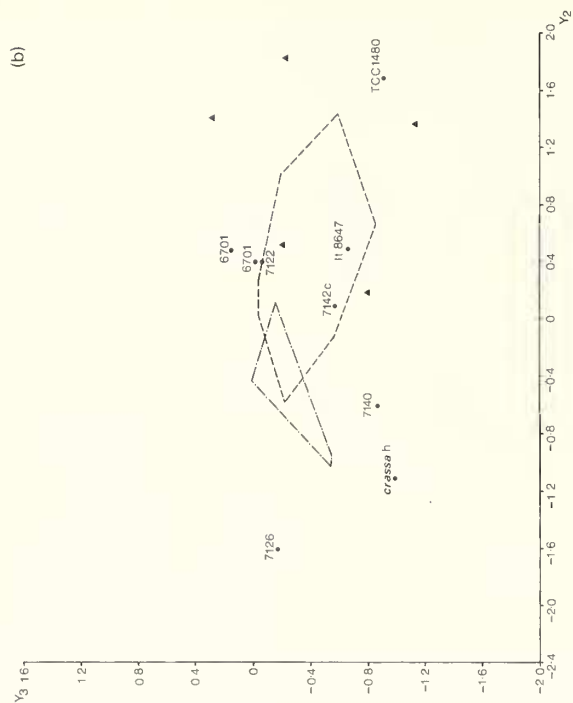
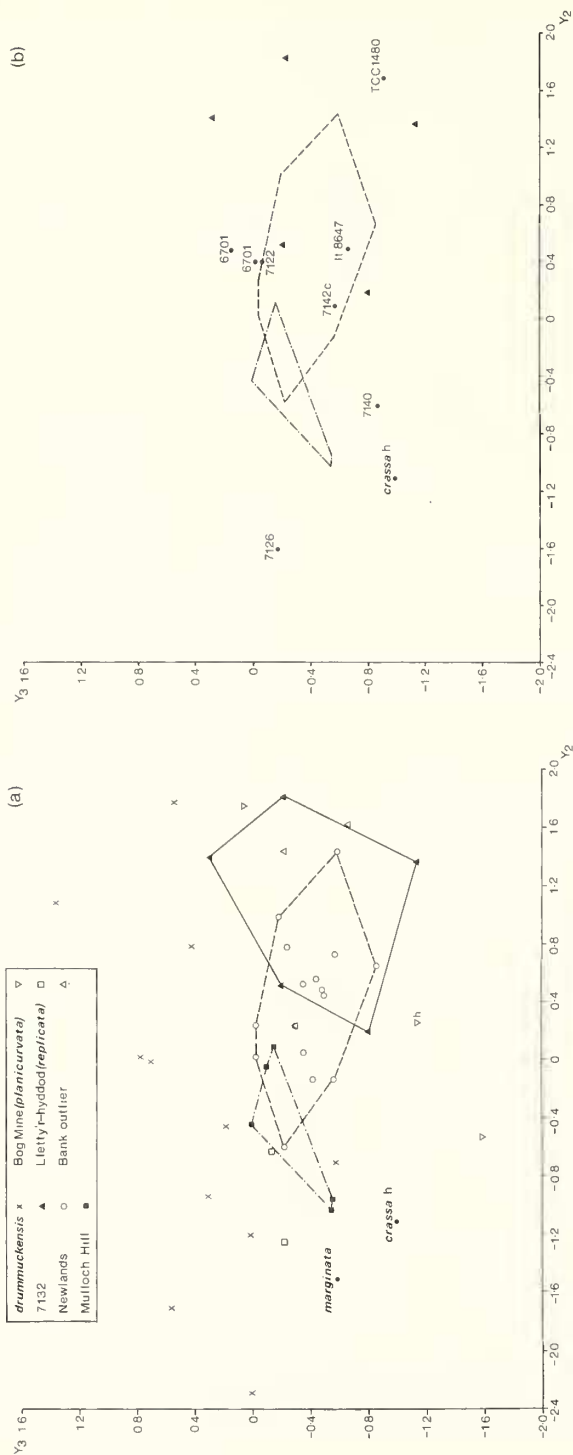
Length and profile of preglabellar area. Variation in the length and profile of the preglabellar area in relation to glabellar length has been investigated by means of a principal components analysis of variates x_1 , x_2 , x_3 , and x_4 . The original data have been transformed to scores on the eigenvectors of the correlation matrix (Table 1a)

TABLE 1. Column eigenvectors y and eigenvalues λ (as percentages) of correlation matrices based on (a) four variates (x_1 to x_4) representing glabellar length and profile of the preglabellar area, and (b) the same four variates with the addition of x_5 (maximum glabellar width). The same data, based on the collections listed in text-fig. 2, are used in both analyses. In the last column of (a) are shown the standard deviations σ of x_1 to x_4 , by means of which additional specimens could if required be plotted on text-fig. 2.

(a)	y_1	y_2	y_3	y_4	σ
x_1	0.570	-0.228	-0.128	-0.779	3.0866
x_2	0.555	0.031	-0.660	0.506	0.6773
x_3	0.525	-0.315	0.704	0.361	0.4096
x_4	0.302	0.921	0.231	-0.086	0.1995
λ	69.0	21.6	7.2	2.2	
(b)	y_1	y_2	y_3	y_4	y_5
x_1	0.505	-0.146	-0.090	-0.531	-0.659
x_2	0.479	0.107	-0.604	0.623	-0.076
x_3	0.459	-0.220	0.755	0.412	-0.035
x_4	0.224	0.943	0.209	-0.127	0.037
x_5	0.505	-0.174	-0.116	-0.380	0.747
λ	73.4	18.0	5.8	2.1	0.7

based on the collections listed in text-fig. 2. The direction cosines of the eigenvector (y_1) corresponding to the first principal component (i.e. the largest eigenvalue) are all positive and this eigenvector is taken to be a measure of size. The mutual relations of the samples in the space defined by the remaining three eigenvectors are taken to represent the size-independent shape differences between the samples. Two-dimensional plotting on pairs of eigenvectors can be used to depict these three-dimensional relationships (text-fig. 2a-d). It will be seen from the direction cosines that the second eigenvector (y_2) is a measure of degree of overhang of the preglabellar area (decreasing scores corresponding to increasing overhang), while the third eigenvector (y_3) contrasts height of preglabellar area (increasing scores) with length of preglabellar area (decreasing scores), and the fourth eigenvector (y_4) is a measure of length (and partly of height) of the preglabellar area relative to glabellar length.

Discrimination between the three main early Llandovery samples (Mulloch Hill, Newlands, loc. 7132) is seen from text-fig. 2 to be due almost entirely to the second eigenvector, and the slightly overlapping fields of these samples form a belt almost parallel to the y_2 axis along which there is a progressive increase in degree of overhang of the preglabellar area from loc. 7132 through Newlands to Mulloch Hill. The holotype of *Diacalymene crassa* lies beyond Mulloch Hill on y_2 and is displaced somewhat upwards on y_4 . The Upper Llandovery *C. replicata* specimens plot at or slightly beyond the Mulloch Hill end of the early Llandovery belt, while the Bog Mine (*planicurvata*) and Bank outlier specimens partly overlap Newlands and loc. 7132. When the Welsh early Llandovery specimens including loc. 7132 are plotted (text-fig. 2b, d) they form a belt elongated along y_2 and slightly displaced upwards on y_4 relative to Mulloch



Hill and Newlands. Several of the Welsh early Llandovery specimens (locs. 6701, 7122, 7142c, specimens It 8647, TCC 1480) cluster at the loc. 7132 end of this belt, but there is no clearly defined hiatus between these specimens and the isolated specimens (from locs. 7126, 7140) plotting near *D. crassa*.

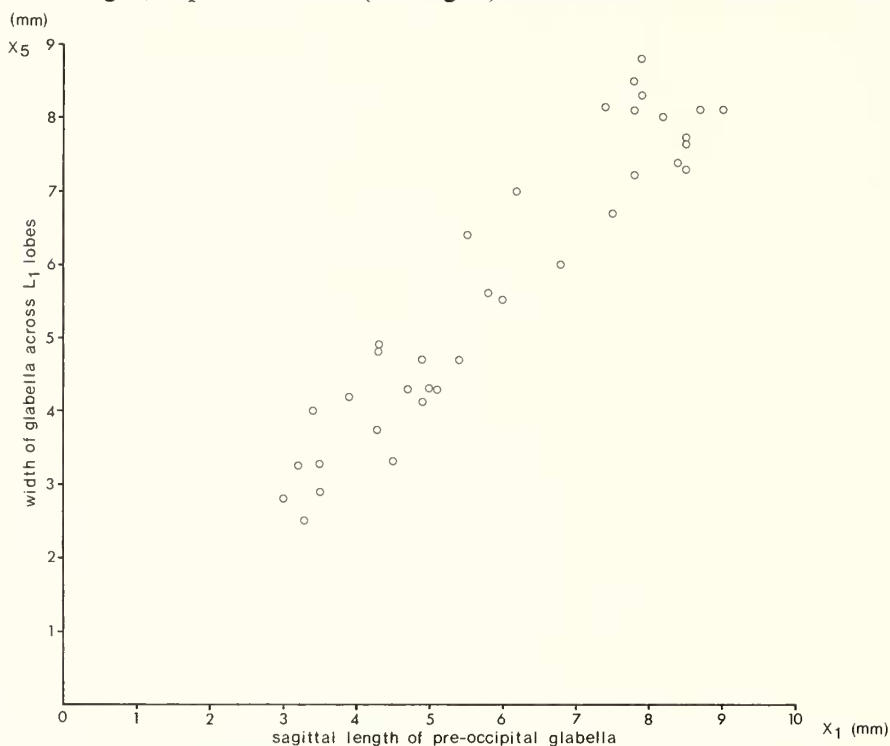
The y_4 axis of the correlation matrix has an appreciable loading on x_3 as well as on x_2 , and in order to determine how much these two variables contribute separately to the upward displacement of the Welsh specimens on y_4 it is necessary to turn to a principal components analysis of the covariance matrix derived from the same data as the correlation matrix. The second and third eigenvectors of the covariance matrix have direction cosines of $(-0.165, 0.936, -0.166, 0.264)$ and $(-0.132, 0.110, 0.975, 0.141)$ and can thus serve as indices of variation in x_2 and x_3 separately. The mean scores of the Mulloch Hill, Newlands, and combined Welsh samples on these two eigenvectors are respectively $(-0.11, -0.17)$, $(0.14, -0.19)$, $(0.47, -0.02)$. There are significant differences on covariance y_2 between all three samples ($p < 0.005$ in both cases on rank sum tests), but on covariance y_3 only the Welsh specimens differ significantly ($0.005 < p < 0.010$). Welsh specimens thus have both longer and higher preglabellar areas than Scottish specimens, while among the latter Newlands specimens have longer preglabellar areas than do specimens from Mulloch Hill. Also included in the principal components analysis were two Upper Ordovician species *Diacalymene marginata* Shirley and *Calymene drummuckensis* Reed which are plotted on text-fig. 2 and are discussed further below. Another aspect of the variation in profile of the preglabellar area is the presence or absence of a 'ridge'. As considerable taxonomic significance has been attached to this feature discussion of it is deferred until the taxonomy of the samples is considered (see p. 147).

Inclination of preglabellar area. The only objective measure of this feature is that given by x_6 and even this is not entirely satisfactory because of the difficulty of measuring it accurately, particularly on large specimens: it shows considerable variation, the extreme range of x_6 over all samples being 138° to 173° , although only three out of twenty-four specimens lie beyond the range 150° to 165° . The range of Newlands values (134° to 165°) includes the holotypes of *crassa* and *planicurvata*, the two measurable topotypes of *replicata*, all the Mulloch Hill specimens, and all except one specimen from loc. 7132. There is no evidence that the collections can be satisfactorily differentiated on the basis of this feature.

Relative width of glabella. A plot of width across L_1 (x_5) against preoccipital glabellar length (x_1) shows much scatter with an apparent tendency to group on either side of

TEXT-FIG. 2a-d. Calymenid crania plotted on the second and third (figs. a, b) and second and fourth (figs. c, d) eigenvectors of the correlation matrix for x_1, x_2, x_3 , and x_4 based on collections from Newlands, Mulloch Hill, Thraive Glen (*drummuckensis*), Bog Mine (*planicurvata*), Bank outlier, Lletty'r-hyddod (*replicata*), locs. 6701, 7122, 7132, 7140, 7142c, and specimens GSM 54910 (*crassa* holotype), TCC 1480, It 8647. A topotype of *marginata* (HMA 7334) and a specimen from loc. 7126, although plotted, were not included in the data from which the correlation matrix was calculated. For purposes of clarity the Welsh early Llandovery specimens (except *crassa* holotype and the loc. 7132 sample) have been omitted from figs. a and c, and are shown in figs. b and d together with the perimeters of the Newlands and Mulloch Hill spreads. Holotypes are marked h.

the line representing equality—at least up to a preoccipital glabellar length of about 9 mm beyond which there is insufficient evidence. The phenomenon is also seen when the Newlands sample, in which complications due to tectonic and compaction distortion are slight, is plotted alone (text-fig. 3). The distribution of the ratio x_5/x_1 for



TEXT-FIG. 3. Maximum transverse width of glabella across L_1 (x_5) plotted against sagittal length of pre-occipital glabella (x_1) for the Newlands sample.

the combined Llandovery samples (excluding distorted specimens), grouped at intervals of 0.05 between 0.7 and 1.2 (lower limits of classes) is 1, 1, 4, 11, 12, 6, 7, 9, 6, 2, 2, with a suggestion of a crude bimodality around equality of length and width.

Variation in this character can, however, be more elegantly analysed by principal components analysis, which demonstrates both the bimodality of relative glabellar width and the fact that variation in this character is independent of the previously analysed variation in the profile of the preglabellar area. On rerunning the principal components analysis with the same data but with x_5 added to the four variates (x_1 to x_4) used earlier, there are now five eigenvectors of a 5-variate correlation matrix (Table 1b). It will be seen that, relative to the x_{1-4} axes, the first four 5-variate eigenvectors are orientated very close to the four 4-variate eigenvectors: they clearly correspond to these four eigenvectors, and if the data of text-fig. 2 are replotted on 5-variate (instead of 4-variate) y_2 , y_3 , and y_4 axes the mutual relations of the points are only negligibly altered. The fifth 5-variate eigenvector, on the other hand, is seen from its direction cosines to be concerned almost exclusively with relative glabellar

width, its loadings on x_2 , x_3 , and x_4 which measure the preglabellar profile being very small. Furthermore, the scores of the pooled samples on the fifth eigenvector are bimodally distributed, the frequencies of scores grouped at intervals of 0.05 between -0.5 and $+0.3$ (lower limits of classes) being 1, 0, 1, 8, 5, 6, 4, 0, 2, 10, 8, 2, 1, 2, 1, 1, 1: the zero near the middle corresponds to the interval from -0.15 to -0.10 , the gap being adjacent scores being from -0.1709 to -0.0668 . The fifth eigenvector produces therefore a clustering into wide and narrow glabellas more convincing than the clustering based on the x_5/x_1 ratio but corresponding very closely to it: of fifty-three cranidia used in the principal components analysis, only three are classified (into wide or narrow) differently by the two criteria. The fifth eigenvector is by definition at right angles to the other four eigenvectors, in particular to y_2 , y_3 , and y_4 . Variation in relative width of the glabella is thus independent of variation in the profile of the preglabellar area.

Wide and narrow forms are found in all the samples examined, with the exception of the small samples from Bog Mine and Bank where only wide forms occur. The pattern of variation in glabellar width is apparently a simple dimorphism cutting right across the samples, whereas the pattern of variation in profile of the preglabellar area is quite different in that individual samples are homogeneous but differ slightly but consistently from each other. The conclusion seems inescapable that variation in profile of the preglabellar area represents variation between samples in each of which the same two morphs (presumably sexual dimorphs) occur. It is interesting to note that, although the dimorphism is visually very striking (compare for instance the two Newlands cranidia illustrated on Pl. 26, figs. 5 and 9), when the different characters are standardized to unit variance (as in the correlation matrix) variation in this character is considerably less than that of the preglabellar profile (see the percentage eigenvalues in Table 1b). The likelihood of dimorphism in glabellar width complicates comparisons between the samples based on this character, as differences between samples may be due to different proportions of the two morphs in the populations rather than (or as well as) to different length-width growth relations. The distribution of the two morphs is shown in Table 2, and although the numbers

TABLE 2. Numbers of wide and narrow glabellas at different localities, based on scores on y_5 (see Table 1b).

	Narrow	Wide
Newlands	12	4
Mulloch Hill	2	3
Loc. 7132	2	3
Lletty'r-hyddod	1	1
Bog Mine	0	3

involved are small there is a preponderance of narrow forms at Newlands and of wide forms elsewhere ($p = 0.024$, single-tailed, for the contrast between Newlands and the rest).

Free cheek, hypostome, and rostral plate. Free cheeks from Newlands and probably those from loc. 7132 and Mulloch Hill are like the cheek illustrated from Meifod (Temple 1970, pl. 18, fig. 15), that is with a rounded obtuse angle in the outer margin

shortly in front of the posterior extremity of the cheek and with a corresponding angle towards the posterior end of the facial suture. No topotype free cheeks of *crassa* are available but a specimen from the Gasworks Mudstone (TCC 1364), which is probably referable to *crassa* on the basis of its preglabellar area, also shows a free cheek of this kind (Pl. 25, fig. 8). In the holotype of *replicata* the angles in the cheek margin and facial suture appear to be less pronounced, although the cheek margin is slightly imperfect hereabouts. The free cheek of *planicurvata* is unknown.

Except for a fragment from loc. 7132 the hypostome is known only from Newlands. The rostral plate also is known from Newlands and Mulloch Hill and in the holotype and another topotype of *replicata* (Pl. 26, fig. 1): in all these forms it consists of an anterior part, moderately concave (sag. and exsag.) in dorsal view, and a posterior flange directed steeply upwards so that its upper edge lies close beneath the preglabellar furrow. The probable *crassa* specimen mentioned above (TCC 1364—Pl. 25, fig. 6) shows the anterior part of the plate somewhat elongated (sag. and exsag.), but the posterior flange is not visible, presumably as a preservational defect.

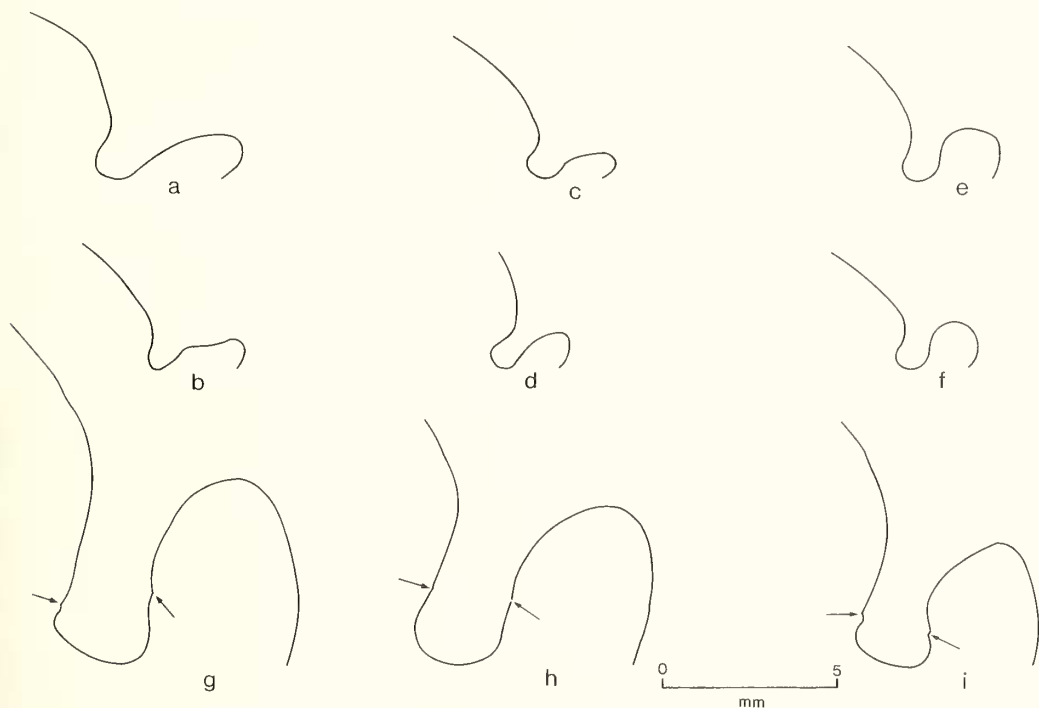
Thorax. Specimens showing the thorax are available for *replicata* (topotype) and probably *crassa* (TCC 1364), and from Newlands and Mulloch Hill: all show the presence of thirteen segments, although TCC 1364 lacks a pygidium to make the count definitive. The thoracic segments are similar in all these forms.

Pygidia. Topotype pygidia are known for *replicata* (Pl. 26, fig. 1) and *planicurvata*, and a pygidium (TCC 1363—Pl. 25, fig. 7) which may belong to *crassa* is found at the same locality as TCC 1364. Pygidia are also found at Newlands and Mulloch Hill. All these pygidia are of the same general type as that described and illustrated from Meifod (Temple 1970, p. 64, pl. 18, figs. 18–20), although the interpleural furrows are usually not as strongly marked on internal moulds or on exteriors as in the relatively small Meifod specimens. The most characteristic feature of all these pygidia is the pair of strong ridges, more or less exsagittally directed, between the fifth pleural furrows and the posterior end of the rachis. Despite the over-all resemblances of all these pygidia there are slight differences in shape between localities: for instance, at Newlands the rachis has a more pointed posterior termination than at loc. 7132 where it is somewhat transversely truncated. Doubtless, detailed biometrical analysis would reveal further differences between samples, although the situation is likely to be complicated (as in cranidia) by the existence of dimorphism of rachial width, as is suggested by the positively skew distribution of the x_8/x_7 ratio in the Newlands sample (compare also the two pygidia illustrated from Meifod—Temple 1970, pl. 18, figs. 18, 20).

Discussion. All the samples of Llandovery age have a number of features in common—the buttressing of L_2 , the outline of the free cheek (doubtful in *replicata*), and the pygidium with strong ridges behind the fifth pleural furrows. Some variation within samples (as in glabellar and rachial width) may be attributable to dimorphism, but the greatest variation between samples concerns the length and profile of the preglabellar area. The latter feature has been used in particular by Shirley (1936) in his important work on calymenid systematics as the distinguishing feature between *Calymene*, to which he referred *replicata*, *planicurvata* and the Newlands sample,

and *Diacalymene*, to which he referred *crassa*, *Diacalymene* being considered to differ from *Calymene* in the possession of a 'ridge' on the preglabellar area (Shirley 1936, p. 396). The type species of *Diacalymene* is *Calymene diademata* Barrande 1846 from the Silurian of Bohemia. A small sample of *C. diademata* from one of the original localities, St. Iwan, Bohemia, preserved largely as internal moulds, has been studied in the British Museum (Natural History). Collections of two Upper Ordovician species, referred to *Diacalymene* by Shirley, have also been studied, firstly a sample (mainly internal moulds) of *Calymene drummuckensis* Reed (1906, p. 135, pl. 17, fig. 14; pl. 18, figs. 1-4) from the Upper Drummuck Beds (Ashgill), Thraive Glen, Girvan (British Museum (Natural History)), and secondly a topotype cranidium (internal and external moulds (HMA 7334)) of the slightly earlier *Diacalymene marginata* Shirley 1936 (p. 415, pl. 29, figs. 19-20) from the Lower Drummuck Beds, Quarrel Hill, Girvan.

The preglabellar area of *diademata* is relatively steeply inclined, with values of 140° , 148° , 150° for x_6 in three cranidia: it culminates in a transverse keel (text-fig. 4g, h, i), variably subangular to rounded in section, in front of which its anterior slope is steep but not strongly overturned in front (in the orientation of text-fig. 4).



TEXT-FIG. 4. Right sagittal profiles of preglabellar areas of calymenid species which have been referred to *Diacalymene*. The profiles are orientated so that the tangent from the rostral suture to the base of the preglabellar furrow is horizontal. Profiles are drawn from sagittally sectioned silicone rubber casts of internal moulds; integument about 0.2 mm thick is present in the bases of the preglabellar furrows below the small arrows in profiles (g)–(i). (a) *crassa* holotype, GSM 54910, (b) *crassa*, Zs 960, from loc. 7140, (c) *marginata* topotype, HMA 7334, (d)–(f) *drummuckensis* from Thraive Glen, respectively In 23372, In 46668, In 41344; (g)–(i) *diademata* from St. Iwan, Bohemia, respectively In 42354, In 19894, In 59826.

The keel is developed only rarely in *drummuckensis* (text-fig. 4d), the preglabellar area in this species being commonly rounded in section (text-fig. 4e, f) and overhanging in front. In *crassa* (text-fig. 4a, b) and *marginata* (text-fig. 4c) the keel appears to be represented by the overhanging anterior margin of the cranidium, and it is thus more acute and more forwardly directed than in *diademata*.

As the term is interpreted here, the 'ridge' mentioned by Shirley as diagnostic of *Diacalymene* is a different structure from the keel, being situated further back than the keel and just in front of the preglabellar furrow. It is best developed in the topotype *marginata* (text-fig. 4c), in the paratype of *crassa* (GSM 54911), and in a loc. 7140 specimen referred to *crassa* (Pl. 25, fig. 2; text-fig. 4b), although in the holotype of *crassa* (Pl. 25, figs. 3-4) the ridge is less clearly marked and is not unequivocally discernible in sagittal section—perhaps because of slight abrasion (text-fig. 4a). In all these specimens in which the ridge is well developed the anterior part of the preglabellar area is flattened in profile, and the ridge represents the break in slope that delimits the flattened part posteriorly and separates it from the preglabellar furrow. For this reason a slight ridge is developed in one specimen from loc. 7132 in which there is incipient flattening of the anterior part of the preglabellar area. Of three Bohemian specimens of *diademata* in which the preglabellar furrow has been cleared of matrix, one shows a ridge as a broad rounded angulation slightly more than half-way down the convex backward-facing slope of the preglabellar area (text-fig. 4i), but in the other two specimens this backward slope is more evenly convex throughout its profile and there is little indication of a ridge. (The presence of integument at the bases of the preglabellar furrows of these two specimens may also help to obscure the ridges, but even if allowance is made for this factor the ridges must be very diffuse.) In specimens of *drummuckensis* (text-fig. 4d-f) the back slope of the preglabellar area is also convex in profile, either evenly so throughout the profile, or occasionally with sharper curvature locally to produce a slight ridge. It is clear that the preglabellar areas of both *diademata* and *drummuckensis* are very variable in profile (see also below for quantitative assessment of this variability in *drummuckensis*). This variability, taken together with the subjectivity involved in judging whether a particular specimen is ridged or not, apparently vitiates the use of ridging as a diagnostic character of *Diacalymene*, at least for the discrimination of internal moulds.

The three measured specimens of *diademata* are very large compared with most of the Llandovery specimens measured, so that projection of them on to the shape eigenvectors of the correlation matrix (text-fig. 2) involves error due to size extrapolation. They plot, however, so far off the top of the diagrams, with scores (y_2 , y_3 , y_4) of respectively (-2.62, 2.70, 2.30), (1.89, 5.18, 2.81), (0.65, 2.90, 2.11), as to indicate a fundamental shape difference from the Llandovery samples: their high scores on y_3 reflect the relative shortness and height of the preglabellar area of *diademata*. The *drummuckensis* sample is closer to the Llandovery samples, forming a belt displaced upwards on y_3 and with wide but apparently continuous variation in y_2 scores. This great variation in y_2 can be partly explained by the fact that the size eigenvector of the *drummuckensis* sample (direction cosines 0.580, 0.575, 0.576, 0.014) is differently orientated from that of the pooled samples. Nevertheless, although the range of *drummuckensis* scores on the *drummuckensis* y_2 (direction

cosines -0.049 , -0.112 , 0.136 , 0.983) is much less than on the pooled y_2 , it is still greater than that of, for instance, Newlands scores on the pooled y_2 : *drummuckensis* shows considerable variability in degree of overhang of the preglabellar area. The topotype of *marginata* plots near to *crassa* as a continuation of the Mulloch Hill-Newlands-loc. 7132 spread.

It is hazardous to attempt phylogenetic interpretation on the basis of the present limited studies, but the principal components analysis suggests that it is more plausible to link *marginata* and *crassa* with the Llandovery belt of variation covering Mulloch Hill-Newlands-loc. 7132, than via the Upper Ordovician *drummuckensis* with the morphologically distant *diademata*. Both *crassa* and *marginata* are therefore removed from *Diacalymene* and referred to *Calymene* s.l., although the assignment is provisional until the profile of *C. blumenbachi* has been analysed.

The stratigraphical sequence of the four Girvan samples investigated is (from bottom to top) *marginata*-*drummuckensis*-Mulloch Hill-Newlands. The relations in text-fig. 2 suggests the possibility of evolution at Girvan from *marginata* (with *drummuckensis* as a temporary offshoot) through Mulloch Hill to Newlands. Furthermore, since *marginata* has been widely reported from the Ashgill of England and Wales (Shirley 1936, p. 416; Ingham 1966, p. 498) it is possible to envisage a link by migration between *marginata* and *crassa* from the early Llandovery of Wales. At Haverfordwest the loc. 7132 sample, which appears to be morphologically more advanced even than Newlands on an evolutionary interpretation of the y_2 changes, occurs high in the Gasworks Mudstone. In this case, though, there is no evidence of an evolutionary sequence leading up to it, for the stratigraphical succession of the other Gasworks Mudstone localities (compare text-fig. 2) is (from bottom to top) 7122-7142c-7140-TCC 1480-7126-7132, with an apparently haphazard sequence of y_2 scores. In any case there can be no long-term evolutionary sequence along y_2 in Wales because the Upper Llandovery *replicata* specimens come at the wrong end of the belt of variation. The slightly higher Welsh than Scottish scores on y_4 in early Llandovery forms presumably represent geographical variation in the length and height of the preglabellar area.

Formal taxonomic treatment of the early Llandovery calymenids at specific level is hindered by the inadequacy of the type collections of *crassa*, *replicata*, and *planicurvata*. Indeed, of the collections studied, only the Newlands material, which ironically bears no formal name, is adequate to form the basis of a species, and it is beyond the scope of the present work to establish a taxon for this sample. In the absence of knowledge of variation at most of the Welsh early Llandovery localities neither the statistical nor the biological relations of the samples can be inferred with confidence and any taxonomic decision must be arbitrary.

The grouping of the Welsh specimens adopted here is into two subjectively delimited species, namely *Calymene crassa* based upon the holotype of that species, and *Calymene* sp. A based upon the loc. 7132 sample.

Genus *CALYMENE* Brongniart, 1822*Calymene crassa* (Shirley, 1936)

Plate 25, figs. 1-8; text-fig. 4a

1936 *Diacalymene crassa* sp. nov. Shirley, p. 416, pl. 29, figs. 21-23.non 1970 *Diacalymene* sp. [*crassa* Shirley, 1936]; Temple, p. 64, pl. 18, figs. 13-20 [= *Calymene* sp. A—see below].*Holotype*. Internal mould of cranidium, GSM 54910 (ex Pg. 2364), from Gasworks Mudstone, side of Frolic Path, 383-390 yd SE. of Higgon's Well, Haverfordwest, Pembrokeshire.*Paratype*. Internal mould of cranidium, GSM 54911 (ex TCC 1776), from brook 400 yd SE. of Cotts Park, 1½ miles E. of Haverfordwest, Pembrokeshire.*Localities and material*. Locs. 7004b (cranidium), 7022a (cranidium, ? free cheek), 7029a (cranidium), 7126 (cranidium), 7140 (two cranidia, ? free cheek, ? thoracic segment); TCC 1363 (pygidium), TCC 1364 (cephalon and thorax) from Gasworks Mudstone, lane leading to Gasworks, Haverfordwest, Pembrokeshire, at 93 yd from [gas lamp at] junction with New Road.*Measurements* (mm)

		x ₁	x ₂	x ₃	x ₄	x ₅	x ₆
Holotype	GSM 54910	10.6	2.8	1.2	0.1	10.7	162°

Remarks. In the absence of a topotype sample from which to assess variation, the limits of this species must be entirely subjective. As interpreted here, the features distinguishing internal moulds of *crassa* from those of *Calymene* sp. A are the flattened profile of the anterior part of the preglabellar area, the resulting accentuation of the ridge which delimits the flattened part posteriorly, and the tendency of the preglabellar area to overhang in front. These qualitative differences from sp. A show up quantitatively primarily by low scores on y₂, but neither qualitatively nor quantitatively is there a clear division between the two species—the loc. 7132 specimen of sp. A which most closely approaches *crassa* in text-fig. 2 also shows incipient flattening of the anterior part of the preglabellar area. Only four specimens other than the holotype are referred to *crassa* with some confidence, namely the paratype GSM 54911 (Shirley 1936, pl. 29, fig. 23), the cranidia illustrated on Pl. 25, figs. 1 and 2 from locs. 7004b and 7140, and a cranidium from loc. 7126. Specimen TCC 1364 (Pl. 25, figs. 5, 6, 8) and a cranidium from loc. 7022a also have the *crassa* type of preglabellar

EXPLANATION OF PLATE 25

All specimens are internal moulds except the original of Fig. 8, and all are from early Llandovery.

Figs. 1-8. *Calymene crassa* (Shirley). 1, cranidium with doublure excavated on right side, Zs 953, × 4, NE. of Meifod (loc. 7004b). 2, cranidium, Zs 960, × 2.5, Haverfordwest (loc. 7140). 3-4, cranidium in dorsal and profile views, holotype, GSM 54910, × 2.5, Haverfordwest. 5, 6, 8, cephalon and thorax in profile view (× 2.5), cephalon in ventral view after excavation of doublure (× 2.5), latex cast of exterior of cheek region (× 5), TCC 1364, Haverfordwest. 7, fragmentary pygidium, TCC 1363, × 4, Haverfordwest.

Figs. 9-13, 15, 16. *Calymene* sp. A. 9-10, cephalon in profile and dorsal views, TCC 1480, × 2.5, Haverfordwest. 11, cranidium, Zs 954, × 3, Haverfordwest (loc. 7132). 12, cranidium, Zs 955, × 2.5, Haverfordwest (loc. 7132). 13, cranidium, Zs 961, × 5, Haverfordwest (loc. 7122). 15, 16, pygidia, Zs 958 and Zs 956, × 2.5, Haverfordwest (loc. 7132).

Fig. 14. *Calymene* sp. indet. Pygidium, Zs 959, × 2.5, Haverfordwest (loc. 7121).



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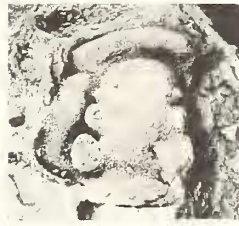
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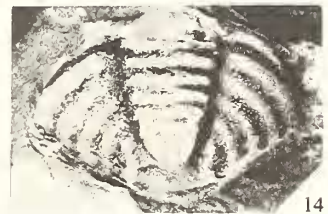
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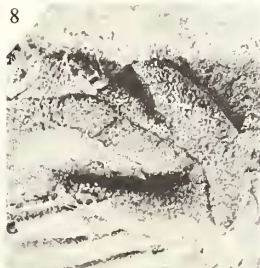
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area, but both are crushed in front and the sharpness and overhang of their cranidial margins have been accentuated by crushing: it is unlikely, though, that their condition could have been produced from a profile that was initially not overhanging to some extent. Specimen TCC 1364 and the pygidium from the same locality (TCC 1363) are important because they provide the only available information on free cheeks, rostral plate, thorax, and pygidium of *crassa*. There is no evidence that in any of these features *crassa* differs from *Calymene* sp. A.

Calymene sp. A

Plate 25, figs. 9–13, 15, 16; Plate 26, figs. 5–6, 9–10

- 1906 *Calymene blumenbachi* Brongniart, 1822 [partim]; Reed, p. 133, pl. 17, fig. 13.
 1936 *Calymene replicata* sp. nov. [partim—Newlands material], Shirley, p. 411.
 1970 *Diacalymene* sp. [*?crassa* Shirley, 1936]; Temple, p. 64, pl. 18, figs. 13–20.

Localities and material. Locs. 6701, 7021b, 7122, 7132 (abundant but fragmentary), 7142c, 7148; TCC 1480 (cephalon) from Gasworks Mudstone, lane leading to Gasworks, Haverfordwest, Pembrokeshire, at 138 yd from [gas lamp at] junction with New Road; Newlands Formation, Newlands, Girvan.

Remarks. This species differs from *C. crassa* in having a preglabellar area which, although variable, is not as overhanging in front, and of which the anterior part often develops into a roll-like border. The description of the Meifod material (Temple 1970) may be taken as applying to all the Welsh collections with the proviso noted above about the indistinctness in most specimens of the interpleural furrows of the pygidium.

The type locality is loc. 7132 at Haverfordwest, but even here, the most prolific Welsh locality, the material is not adequate to justify formal establishment of a species. The Newlands sample is arbitrarily referred to sp. A on the basis of its overlap with the Welsh sample on the principal components plots, but it differs slightly from sp. A on both y_2 and y_4 scores. The Mulloch Hill sample, which itself overlaps with Newlands, is equally arbitrarily excluded from sp. A. Collection of an adequate topotype sample of *Calymene planicurvata* Shirley may show that this species is close to or identical with sp. A, but *C. replicata* Shirley differs considerably from sp. A in y_2 scores.

EXPLANATION OF PLATE 26

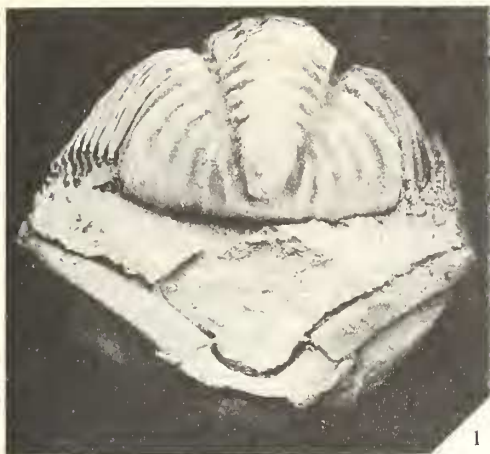
All specimens are internal moulds except the original of Fig. 7, and all are from early Llandovery unless stated otherwise.

Fig. 1. *Calymene replicata* Shirley. Pygidium and ventral view of cephalon of enrolled specimen, topotype A 14923, $\times 2.5$, Lletty'r-hyddod, Llandovery area (Upper Llandovery).

Figs. 2–4, 7–8. *Calymene* sp. Mulloch Hill Beds, Mulloch Hill, Girvan. 2–3, cranidium in dorsal and profile views, In 47724, $\times 2.5$. 4, 7, cephalon and thorax in profile view, latex cast of exterior of cheek region, In 23332, $\times 2.5$. 8, pygidium, In 47696, $\times 2.5$.

Figs. 5–6, 9–10. *Calymene* sp. A. Saugh Hill Beds (Middle Llandovery), Newlands, Girvan. 5, cranidium with narrow glabella, In 43631, $\times 2.5$. 6, free cheek, In 43655, $\times 3$. 9, cranidium with wide glabella, In 43662, $\times 2.5$. 10, pygidium, In 43669, $\times 3$.

Figs. 11–14. *Dalmanites* sp. 11, cranidium, Zs 949, $\times 3$, Haverfordwest (loc. 7127). 12, cranidium, Zs 951, $\times 2$, Haverfordwest (loc. 7126). 13, fixed cheek, Zs 952, $\times 2$, Haverfordwest (loc. 7127). 14, pygidium, Zs 950, $\times 4$, Haverfordwest (loc. 7127).



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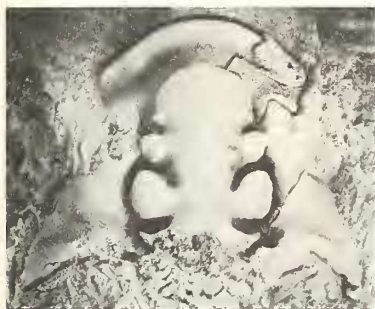
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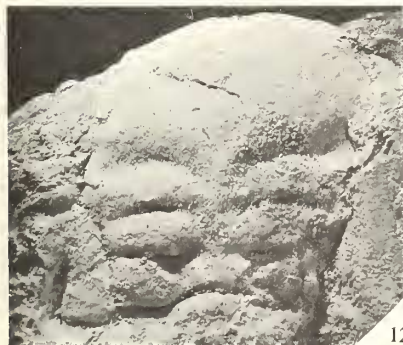
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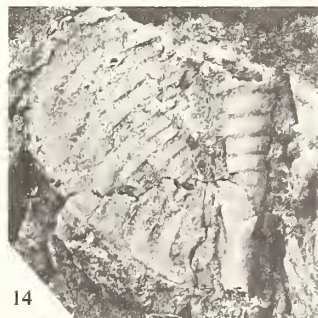
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Calymene sp. indet.

Plate 25, fig. 14

Remarks. Cranidia too poorly preserved for identification, and other parts of the exoskeleton (e.g. pygidia) not diagnostic of either calymenid species recognized, occur at many localities in the early Llandovery of Wales. The figured pygidium, although listed here, may in fact belong to *C. crassa*. It comes from loc. 7121 which is characterized by the occurrence of numerous valves of *Katastrophomena*. The only other locality in the Haverfordwest area (or indeed anywhere in Wales) where abundant *Katastrophomena* are found is a short distance upstream from loc. 7121 at what is probably the type locality of *C. crassa*: the latter may therefore be at the same stratigraphical horizon as loc. 7121, and the calymenids at the two localities may be the same species.

Family HOMALONOTIDAE Chapman, 1890

Genus BRONGNIARTELLA Reed, 1918

Brongniartella sp.

Plate 27, fig. 9

1914 *Homalonotus* sp.; Strahan *et al.*, p. 95.

Remarks. A single damaged pygidium is known from the Gasworks Mudstone at Haverfordwest in the collections of the Institute of Geological Sciences (OTJ 493). The shape and proportions of the rachis and the probable presence of seven pleural furrows are suggestive of *B. platynotus* (Dalman), a species widely spread in Upper Ashgillian strata (Kielan 1960, p. 116, pl. 19, figs. 1-3).

Superfamily CHEIRURACEA Hawle and Corda, 1847

Family CHEIRURIDAE Hawle and Corda, 1847

Genus HADROMEROS Lane, 1971

Hadromeros elongatus (Reed, 1931)

Plate 27, figs. 5, 6, 8

?1851 *Ceraurus Williamsi* (M'Coy); M'Coy, p. 155, pl. 1F, figs. 13, 13a-b.

EXPLANATION OF PLATE 27

All specimens except the original of Fig. 11 are internal moulds, and all except the original of Fig. 10 are from the early Llandovery of the Haverfordwest area.

Figs. 1-4. *Acernaspis* sp. 1, cheek and eye, A 32364, $\times 5$, Gasworks Sandstone, Gasworks. 4, eye of same specimen enlarged, $\times 10$. 2, cranidium, TCC 1533, $\times 6$, Gasworks Road, 161 yd S. of gas lamp at junction of New Road and Gasworks Road. 3, thorax and pygidium, OTJ 278, $\times 4$, 20 yd S. of stream, 480 yd W. of Black Backs Bridge.

Figs. 5, 6, 8. *Hadromeros elongatus* (Reed). Priory Mill railway cutting, 80 yd S. from level crossing. 5, 8, cranidium in dorsal and profile views, OTJ 612, $\times 2$. 6, cranidium, OTJ 611, $\times 2$.

Fig. 7. *Stenopareia* sp. Right free cheek, Zs 962, $\times 2$. Haverfordwest (loc. 7126).

Fig. 9. *Brongniartella* sp. Pygidium, OTJ 493, $\times 1.1$. Riverside, 235 yd SE. of gate at Higgon's Well.

Fig. 10. *Ceratarginae* indet. Hypostome, Zs 963, $\times 12.5$. WNW. of Llandysilio (loc. 7001a).

Figs. 11, 12. *Odontopleurinae* indet. 11, external mould of pygidium, Zs 957, $\times 6$, Haverfordwest (loc. 7132). 12, cephalon, A 32356, $\times 2$, opposite entrance to Gasworks (Turnbull Collection).



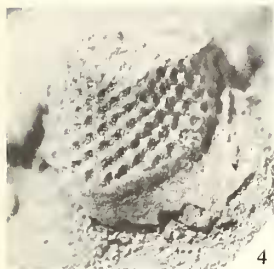
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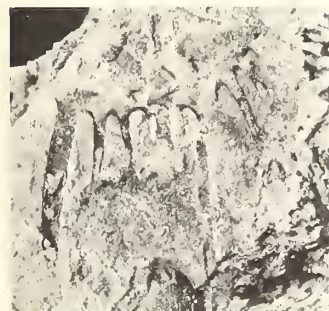
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- 1914 *Cheirurus* sp.; Strahan *et al.*, p. 95.
 1914 *Lichas* sp.; Strahan *et al.*, p. 95.
 1931 *Cheirurus elongatus* sp. n. Reed, p. 103, pl. 4, figs. 5-7; pl. 5, fig. 4.
 1935 *Cheirurus conjunctus* sp. nov. Reed, p. 55, pl. 4, fig. 1.
 1970 *Cheirurus* sp.; Temple, p. 65, pl. 19, figs. 11-12.
 1971 *Hadromeros elongatus* (Reed, 1931); Lane, p. 28, pl. 5, figs. 1-14, 16, 17.

Remarks. No additional cheirurid specimens have been obtained, but there are two fairly good cranidia from Haverfordwest in the collections of the Institute of Geological Sciences. These specimens and those illustrated earlier from Meifod are referred to Reed's species from Newlands, Girvan, on the basis of the backward position (opposite S_1) of the posterior end of the eye. In this respect the specimens from the Lower Llandovery of Skelgill, Westmorland, referred by Lane (1971, p. 30, pl. 4, figs. 5-12) to *H. aff. elongatus*, in which the eye reaches less far back, are closer to *H. keisleyensis* (Reed). Unfortunately no pygidia are known from the Welsh early Llandovery except for M'Coy's poor specimen from the Llandovery area which is only tentatively included in the synonymy.

Superfamily PHACOPACEA Hawle and Corda, 1847

Family PHACOPIDAE Hawle and Corda, 1847

Genus ACERNASPIS Campbell, 1967

Acernaspis sp.

Plate 27, figs. 1-4

- 1970 *Acernaspis* sp.; Temple, p. 68, pl. 18, figs. 10-12, 21.

Remarks. In addition to the material described from Meifod, specimens of *Acernaspis* are known from Llandysilio (loc. 7001a) and Haverfordwest (locs. 7123, 7128, 7147; collections of the Institute of Geological Sciences and the Sedgwick Museum). The material, however, is inadequate either for an assessment of the conspecificity of the different samples, or for comparisons to be made with the finely distinguished species recently described by Männil (1970) from the Lower and Middle Llandovery of Estonia and with the older established *A. elliptifrons* Esmark from the Lower Llandovery of the Oslo region. A specimen from loc. 7123 gave a lens count in vertical files of 4556666.... The illustrated specimen from Haverfordwest (Pl. 27, figs. 1, 4) has seventeen files, of which only the anterior three (567 lenses respectively) are preserved complete, the remaining files showing minimal lens counts of 76676566554332.

Family DALMANITIDAE Vogdes, 1890

Genus DALMANITES Barrande, 1852

Dalmanites sp.

Plate 26, figs. 11-14

Localities and material. Loc. 7126 (cranidium, hypostome), loc. 7127 (cranidium, fixed cheek, pygidium).

Description. The loc. 7127 cranidium (Pl. 26, fig. 11) is an estimated 12 mm long and slightly obliquely distorted. Its palpebral lobe, well preserved on the left side, reaches back to opposite the S_1 furrow, and there is a narrow limb around the glabella behind the facial suture. The glabellar lobation is better seen on the larger cranidium (length

approx. 22 mm) from loc. 7126 (Pl. 26, fig. 12). The fixed cheek bears a strong, tapering genal spine. The poorly preserved pygidium is incomplete but originally about 10 mm long, with apparently nine (possibly ten) pleurae. The rachis terminates roundedly approximately 2 mm from the posterior margin, and behind it there is a raised, axially ridged, posteriorly declining post-rachis which apparently continues to the posterior margin and probably slightly beyond into a small mucro.

Remarks. These specimens from Haverfordwest, which are assumed to be conspecific, are the only dalmanitids known in the present collections. The species they represent shows affinity with the Upper Llandovery *Dalmanites vulgaris* (Salter) var. Whittard (1938, p. 133, pl. 5, figs. 15–16). The pygidium of the latter, which is larger than the loc. 7127 specimen, has ten pleurae in contrast to a probable nine, but agrees in showing the rachis terminating well within the margin, a ridged post-rachis, and a small mucro. The Haverfordwest specimens are referred to *Dalmanites* on the basis of the well-defined posterior termination of the pygidial rachis. This is a feature that is found in *Dalmanites* but is developed only incipiently in *Dalmanitina*, where the rachis continues with little interruption into the posterior spine. In some *Dalmanitina mucronata* (Brongniart), as in the pygidium from the St. Martin's Cemetery Beds (?basal Llandovery) of Haverfordwest (Temple 1952, pl. 2, fig. 4), the rachis is posteriorly terminated, although at a point closer to the margin than in the loc. 7127 specimen. It seems likely that there is a gradation within the early Llandovery from *Dalmanitina* to *Dalmanites*.

Superfamily ILLAENACEA Hawle and Corda, 1847

Family ILLAENIDAE Hawle and Corda, 1847

Genus STENOPAREIA Holm, 1886

Stenopareia sp.

Plate 27, fig. 7

1970 *Stenopareia* sp.; Temple, p. 63, pl. 18, figs. 2–6.

Remarks. Two free cheeks from loc. 7126, where also occurs a pygidium of *Stenopareia* sp., are presumably referable to this species and are larger and better preserved than the single cheek known from Meifod. They show the doublure widening rapidly in front, at the same time becoming concave in dorsal view and developing strong terraced lines such as are found on the rostral plate (Temple 1970, pl. 18, fig. 4).

Superfamily ODONTOPLEURACEA Burmeister, 1843

Family ODONTOPLEURIDAE Burmeister, 1843

Subfamily ODONTOPLEURINAE Burmeister, 1843

Odontopleurinae indet.

Plate 27, figs. 11, 12

Remarks. Two pygidia, from Cefn Rhyddan (loc. 7021c) and the Gasworks Mudstone (loc. 7132), show well-differentiated major spines with two pairs of secondary spines adaxially to them and three pairs abaxially; the Gasworks specimen also shows a further small spine or process at the antero-lateral corner of the pygidium. A similar

pattern of pygidial spines, the anteriormost being more or less distinctly developed, is found in several Ordovician and Silurian members of the Odontopleurinae. The closest stratigraphically to the present occurrences are '*Acidaspis*' *shanensis* Reed (1915, p. 80, pl. 12, figs. 1-11) from the Lower Llandovery of Burma, an undescribed form related to *Leonaspis girvanensis* (Reed) from the Basal Silurian of Watley Gill, Cautley, Yorkshire, and ?*Acidaspis* sp. indet. Bruton (1967, p. 235, pl. 35, fig. 13) from the Upper Llandovery of Estonia. The Welsh specimens are too imperfect for detailed comparison, but appear to be less coarsely granulated than the Yorkshire form; the external surface of the Estonian pygidium is not known.

A very large cephalon in the Sedgwick Museum (A 32356—sagittal length about 15 mm) from opposite the Gasworks entrance at Haverfordwest (Pl. 27, fig. 12) is tentatively associated with the pygidia described above on the basis of its resemblance to the cephalon of the Burmese form. The disparity in size, however, with other odontopleurid cranidia in the collections is such that meaningful comparisons cannot be made with, for instance, the cranidia from Meifod referred to *Leonaspis marklini varbolensis* Bruton (Temple 1970, p. 69, pl. 19, fig. 17). The pygidia of the Meifod form (loc. cit., fig. 13) are clearly different from those described here, so that two forms of Odontopleurinae occur in the Welsh early Llandovery, but the distinguishing characters of the corresponding cephalae are not known.

Superfamily LICHACEA Hawle and Corda, 1847

Family LICHIDAE Hawle and Corda, 1847

Subfamily CERATARGINAE Tripp, 1957

Ceratarginae indet.

Plate 27, fig. 10

Remarks. A small fragmentary cranidium, too poor to illustrate, and a small hypostome are known from loc. 7001a. The hypostome is 2.0 mm in sagittal length and 2.8 mm in maximum width, and has a somewhat asymmetrical posterior margin which is very slightly indented. The subfamily attribution is suggested by Mr. R. P. Tripp who has kindly examined these specimens.

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